

Functional response as a component of dynamic simulation models in biological control: the *Catolaccus*–boll weevil system

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Abstract

A simulation model using Time Varying Distributed Delays was created on the HERMES (Hierarchical Environment for Research Modelling of Ecological Systems) of the USDA/ARS with the purpose of evaluating different forms of functional response components in dynamic simulations of biological control systems. The specific host–parasitoid life system used in the evaluation was the boll weevil–*Catolaccus grandis* system. Four forms of functional response equations were tested: Type I, Type II, a Type II modified to yield constant attack probabilities under constant host:parasitoid ratios, and a temperature-dependent Type II. Simulation runs showed that the parasitoid is potentially capable of considerable suppression of the host population. Predicted host numbers under Type I and II equations did not differ markedly, because realistic host numbers per parasitoid were often found in the linear portion of the Type II equation. The probability of attack using a Type I equation was always near 100% despite arbitrarily increasing the host population to create a wide range of host:parasitoid ratios. The Type II equation resulted in fluctuating attack probabilities which steadily declined as host:parasitoid ratio exceeded 100:1. The modified Type II equation yielded attack probabilities starting at 52% and steadily declining to about 8% when host:parasitoid ratios neared 1000:1. We introduced a realistic, but hypothetical, relationship between functional response and temperature. Simulations using actual weather data from the Rio Grande Valley of Texas suggest that there is little difference between using Types I or II equations, but that the effect of temperature on attack rates is substantial in this system. Caution should be used when incorporating data from experiments into simulation models because experimental conditions are often unrealistically optimal. We discuss the possible importance of temperature and other diurnal or environmental events on functional response and the value of relevant data in this and other simulation models of biological control.

Keywords: Boll weevil; *Catolaccus grandis*; Host–parasite interaction; Pest management

1. Introduction

Simulation modeling has become a standard tool in the analysis of insect predator–prey sys-

tems (Berryman and Pienaar, 1974), especially where the objective of the model concerns biological control. Although a substantial body of literature exists on methods used to model insect development in simulation models (e.g. Wagner et al., 1984; Goodenough and McKinion, 1992), very little has been published regarding the consump-

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tion components required to link the predator and prey submodels (but see Stimac and O'Neil, 1985). Most workers who discuss this parasitism or predation link use a form of functional response equation supported by hypothetical or actual attack rate data. However, the use of attack rates collected in experiments is not always direct because much data collected on parasitism or predation is generational or valid only under the experimental conditions (e.g. host densities, experimental duration) under which the data were gathered. Therefore, these data may not be directly used to calculate the instantaneous attack rates more suited to dynamic simulation models.

Several predator–prey simulation models that incorporate a functional response component are reported in the literature. Acarine predator–prey models have used different forms of the Type II functional response (de Wit and Goudriaan, 1978; Dover et al., 1979; Bernstein, 1985). A particularly complex functional response equation was used by Bernstein (1985) because it incorporates stage-specific predation rates. Mack and Smilowitz (1982a, b) used a temperature-dependent functional response equation in modeling predation by the coccinellid *Coleomegilla maculata* (DeGeer) on the green peach aphid (*Myzus persicae* (Sulzer)). In their model, CMACSIM, predation rate was increased and handling time was decreased as temperature increased from 15.6°C to 32.2°C. The predation rate of the *C. maculata* larvae was also assumed to be linearly related to the log of their biomass. Other such models of predator–prey interactions are the housefly–predator models of Geden et al. (1990) and Wilhoit et al. (1991a). Mathematical models for predation were discussed by Gutierrez and Baumgaertner (1984) and Stimac and O'Neil (1985).

Host–parasitoid models similarly use forms of Type II functional response equations. Griffiths and Holling (1969) used a Type II response in modeling the dynamics of *Pleolophus basizonus* (Grav.) (Ichneumonidae) and the European sawfly, *Neodiprion sertifer* (Geoff.). Their model also included insect distributions and probability of attack, mutual interference among searching parasitoids and competition between parasitoid

progeny within the host. They concluded that the mutual interference component could be ignored because it was significant only at parasitoid densities much higher than those occurring naturally. Hartstack et al. (1976) used an attack probability equation proposed by Knipling and McGuire (1968) in modeling the *Heliothis–Trichogramma* system. Van Batenburg et al. (1983) modeled a eucolid parasitoid of *Drosophila melanogaster* Meig. by incorporating a Type II equation in a Monte Carlo simulation. Wilhoit et al. (1991b) modified a parasite functional response equation of Royama (1971) to become a function solely of the host–parasitoid ratio. Brown et al. (1982) used Leslie matrices to model *Ooencyrtus kuvanae* (Howard) (Hymenoptera: Encyrtidae), an egg parasite of the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae). The matrices were modified to incorporate the effects of insect densities, including mutual interference on parasitism rate.

2. Objectives

Numerous environmental variables such as rainfall, sunlight or wind may reduce parasitoid activity far below that measured under optimal laboratory conditions. For this reason, the direct incorporation into simulation models of functional response parameters not adjusted for these variables will most likely result in over-estimation of attack rates. In this model, we investigate temperature as an environmental variable that affects functional response because its effects on insect activity are well known. We chose this specific host–parasitoid interaction because of the availability of relevant data required to parameterize the model and our familiarity with this system under field conditions. Moreover, the functional response data available are ideal in that they were collected in the field and suited to our objective of simulating insect interactions in realistic situations. These data are also ideal as they were collected daily making them suited to the daily time scale that is typically used in computer simulation models. We must stress at the outset that the model we describe is not meant to

be a predictive model. The objective of the modeling study is the qualitative evaluation of different functional response equations as they related to the *A. grandis*/*C. grandis* interaction. Currently, the model lacks both the complexity and the validation required to be used in a predictive mode, however, it is our long-term objective to develop predictive models for use in management in this and other biological control life-systems.

In this paper, we investigate functional response as a component in dynamic simulations of biological control systems. We evaluate different forms of functional response with regard to their behavior under different host densities or temperature conditions. We compare Type I, Type II and a temperature-dependent Type II equation and assess their effects on the boll weevil (*Anthonomus grandis* Boheman) (Coleoptera:

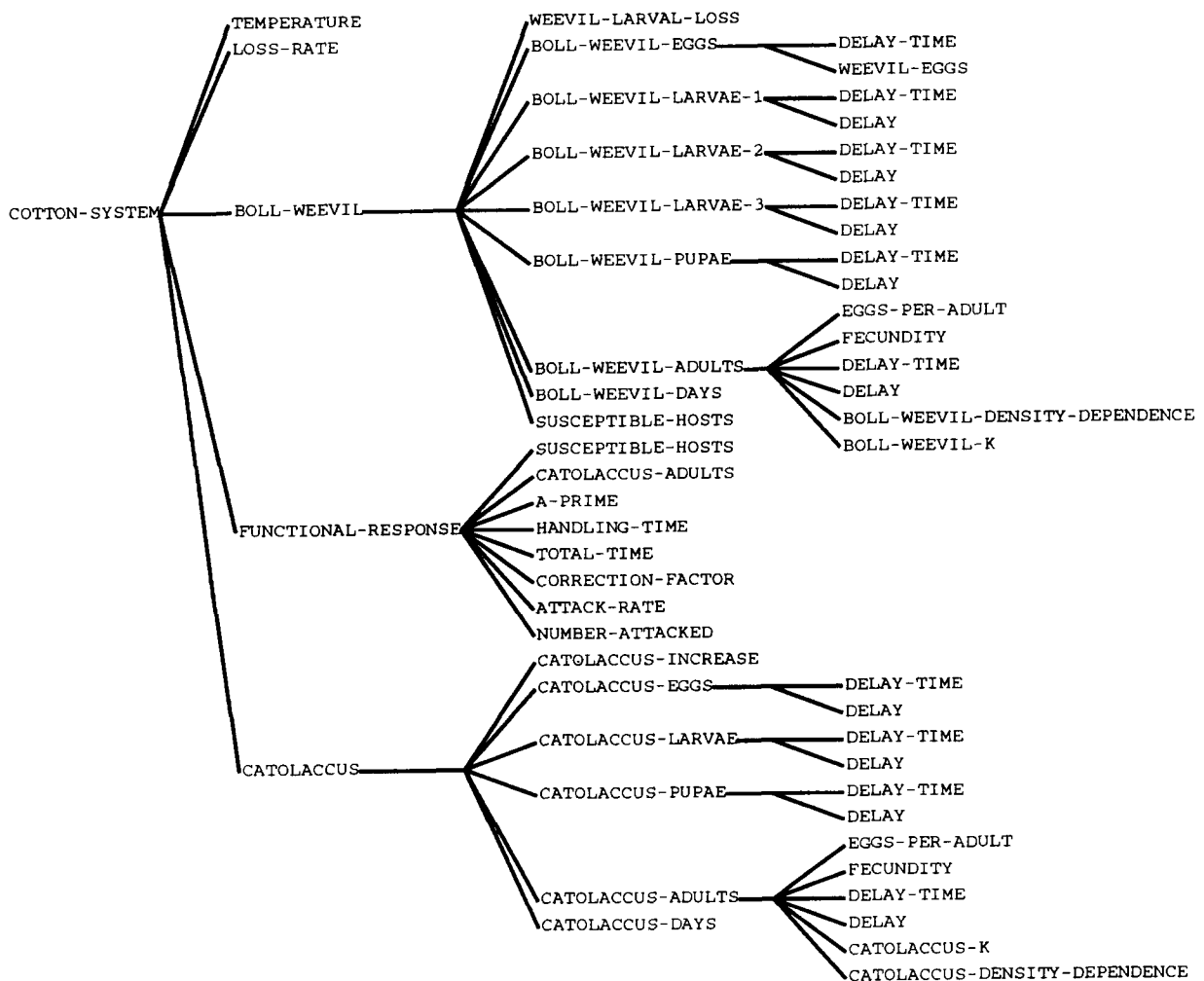


Fig. 1. Display of hierarchical model used for the boll weevil–*Catolaccus* system. Each node in the tree represents a type of model component in the HERMES modeling environment. The model is created by graphically linking the nodes together. Each type of component implements specific methods or computations required based on parameters and inputs and then produces calculated outputs, depending on its type (see Larkin et al. (1988) for details).

Curculionidae)–*Catolaccus grandis* (Burks) (Hymenoptera: Pteromalidae) interaction. We also compare a modified form of the Type II equation which yields constant attack rates when the host:parasitoid ratios are kept constant and densities are altered. Apart from a qualitative evaluation of the effects of different forms of functional response equations, we attempt to explore the applicability of functional response parameters obtained under nearly ideal laboratory conditions to simulation models that attempt to portray realistic host–parasitoid environments where conditions are usually sub-optimal for natural enemy activity.

3. Methods

3.1. The modeling environment

The modeling environment we use is the HERMES system (Hierarchical Environment for Research Modelling of Ecological Systems) of the USDA-ARS. HERMES is written in Common LISP with object-oriented features provided by the Flavors extension of LISP (Symbolics, 1990). The software is implemented on a SymbolicsTM XL1200 computer. Models are created graphically by linking together and parameterizing pre-designed simulation components. Each component represents specific biological stages or processes which can be considered as computational black boxes by the biologist user. These components are linked to form a hierarchy of inter-connected stages or processes that define the simulation model both structurally and computationally (Fig. 1). The inputs and outputs of each component are referred to as *ports* because of the way they may be defined and connected graphically through object-oriented programming methodology. Using this modeling system, the biologist is given the freedom to concentrate on the conceptual problems of the model without having to deal with syntactic constraints as in conventional programming languages. A previous version of HERMES is described in Larkin et al. (1988). A users' guide to HERMES will be available on request (Frodsham et al., unpubl. manual). The

HERMES system is currently being re-compiled to operate on MacintoshTM computers. An IBM PC version is also being considered for development. Several scientifically useful models have been created and evaluated using the HERMES system (e.g. Larkin and Carruthers, 1990; Carruthers et al., 1992; Hajek et al., 1993; Larkin et al., 1995).

3.2. Modeling the boll weevil–*Catolaccus grandis* system

A flowchart representing the combined host–parasitoid life cycle is shown in Fig. 2. The *C. grandis* life cycle is shown on the upper half of the figure and the boll weevil life cycle is below.

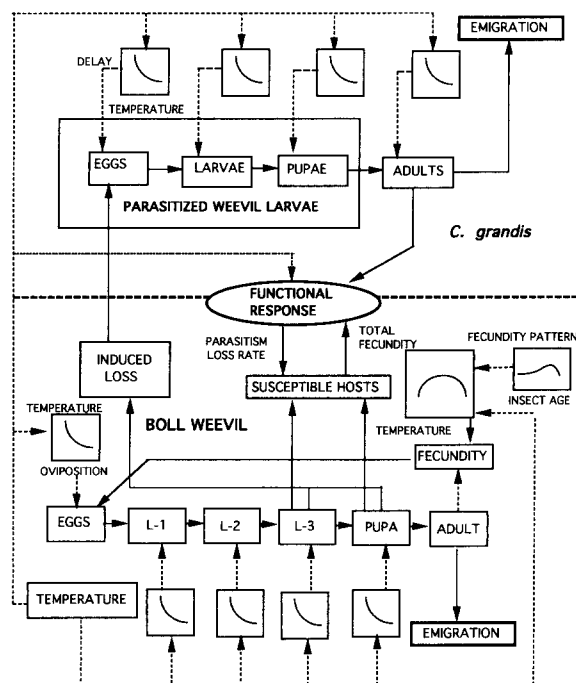


Fig. 2. Flowchart for the boll weevil–*Catolaccus* system. Temperature is required as an input into the lookup tables which calculate an expected delay time according to the temperature at a given time in the simulation. Fecundity is a function of both temperature and a species-specific fecundity pattern. The results of the functional response component are used as the loss rate of the susceptible stages. Both species are assumed subject to adult emigration which increases as the adult population approaches a certain threshold level.

The two populations are linked by the functional response equation which yields a daily attack rate. The attack rate is used as the loss rate of the host population's susceptible stages.

In HERMES, insect development stages are modeled using the Time-Varying Distributed Delay (TVDD) method of Manetsch (1976), modified to include attrition rates (Vansickle, 1977). A TVDD has two important characteristics. First, it accepts an input flow and *delays* it to simulate a development, or delay, process which has a continuously *varying mean time*. Second, it simulates a constant statistical variance in the development period by producing an output flow which *distributes* the input over time to match a selected probability density function. This PDF can have the shape of any member of the family of Erlang curves, which vary from an exponential to a normal distribution. Therefore, the physiological maturation of a population is implemented as a series of delay times, each associated with a specific life stage of the organism. The progression of the population through the series of life stages is distributed rather than discrete because cohorts at a given life stage are not expected to progress to the next stage simultaneously. Moreover, the durations of the various life stages are not constant, but are functions of external factors which change with time, hence the term 'time varying distributed delay'. In insects, the driving variable that most affects developmental times is temperature (Wagner et al., 1984).

For any given developmental delay, a parameter k defines the probability distribution curve which is used to calculate the fraction of the population progressing to the next life stage. A k value of 1 corresponds to an exponential decay, a k of 25 approaches a normal distribution and as k approaches infinity development becomes discrete, i.e. all individuals in a cohort maturing equally. A probability distribution curve with a k value of 20 is thought to be typical of developmental curves associated with many biological organisms, including several insects (Carruthers et al., 1986). The value of k may be estimated by $k = \text{DEL}^2/\sigma^2$ where DEL is the mean delay time and σ^2 is the associated variance obtained in experiments. Because of the mathematics used to

implement TVDDs the parameter k may also be thought to represent the number of sub-stages within each life stage, with corresponding intermediate flow rates between sub-stages. The state or quantity of storage is calculated using the equation:

$$Q(t) = \frac{\text{DEL}}{k} \sum_{i=1}^k r_i(t) \quad (1)$$

where $Q(t)$ is storage at time t , r_i are the intermediate rates, and k and DEL are as previously defined (Manetsch, 1976).

A component type called a *1d-stage* (a HERMES-supplied simulation object) is used to implement developmental computations and consists of a mathematical routine which performs the TVDD calculations and a lookup table specifying the relationship between temperature and delay times. Delay times are estimated during simulation by a linear interpolation between data points or by user-selected means of extrapolation should the temperature exceed the boundary temperatures in the lookup table. A mathematical function may also be used to replace the lookup table (e.g. biophysical model of Sharpe and DeMichele, 1977).

Model instability caused by large rate changes is automatically corrected in HERMES by decreasing the time step for integration which is normally set at 0.1 (i.e. 0.1 of a day). Each TVDD component compares the current delay time with that of the previous time step. A large difference indicates that rates are changing too rapidly and that the Euler integration will be inaccurate if the time step is not reduced. In this case, the TVDD affected calculates a smaller time step using the method described in Abkin and Wolf (1976). After each TVDD has calculated a suitable time step, the smallest one is used for the entire model.

3.3. Parasitoid

The temperature-dependent developmental times of the immature parasitoid stages (Table 1) are taken from Morales-Ramos and Cate (1993, table 1, p. 229). The lookup table for adult

Table 1

Developmental delays of *Catolaccus grandis* (Morales-Ramos and Cate, 1993, table 1, p. 229). Only those parasitoids that completed development under a given temperature were included in the results. Higher temperatures ($\geq 33^\circ\text{C}$) required about twice as many parasitoids to obtain comparable numbers of replicates

Temperature ($^\circ\text{C}$)	Eggs	Larvae	Pupae
18	2.4	16.6	19.5
21	1.6	10.9	10
24	1.4	9.0	8.4
27	1.3	7.4	6.3
30	1.4	6.6	5.3
33	1.1	5.6	5.2
36	0.9	–	–

longevity is (25° 63.55 d, 30° 46.35 d, 35° 20.8 d, 40° 9.0 d) as reported by Morales-Ramos and Cate (1992a). For both insect species, we will assume a 50:50 sex ratio and equal survival rates throughout the simulation periods. Adult sexes will not be modeled separately, but fecundity calculations will be divided in half to account for sex ratio. In the case of *C. grandis*, fecundity is calculated directly from the loss rates due to parasitism of the host population. The loss rates induced in the susceptible stages are added to form the growth rate of the parasitoid egg stage, thus implying a one-to-one correspondence between number of hosts attacked and parasitoids produced.

The adults of both species are assumed subject to density-dependent loss through an emigration component. As the population level of adults approaches a threshold for emigration, the loss rate of adult insects increases according to the equation: loss rate = population level/emigration threshold. This method of introducing a density-dependent loss factor is admittedly an over-simplification and results in increasing emigration as the population level approaches the threshold level, but was used to simplify density-dependence in order to isolate the effects of the functional response component without complications due to other loss factors. No other loss factor was modeled for any other life stage of the parasitoid population.

3.4. Host

The temperature-dependent developmental times for the boll weevil (Table 2) are taken from Bacheler et al. (1975, table 1, p. 809). Because there are no published data on adult longevity, we have assumed a constant longevity at 40 days regardless of temperature, which is probably a slight over-estimate. This assumption makes fecundity less temperature-dependent than it may be in the field. Fecundity of the host is modeled explicitly using a modified *fecundity* component as provided in HERMES. Instead of having *eggs-per-adult* as a parameter (the HERMES default), it is converted to an input table, thus making fecundity temperature-dependent. The relationship between temperature and fecundity (eggs per adult) is (18.3° 41.6, 21.1° 58.5, 23.9° 111.9, 26.7° 179.9, 29.5° 253.5, 32.2° 138.6) with 0 fecundity outside of this temperature range (Cole and Adkisson, 1981). All insect components use the HERMES default value for *k* set at 10 which assumes a distribution slightly skewed to the right (Carruthers et al., 1986). This value is chosen as a reasonable compromise between biological reality, computational speed and data availability. The *fecundity-pattern* (see Fig. 1) represents the proportion of eggs laid during each of the *k* intermediate stages of the adult TVDD. The fecundity pattern used for *A. grandis* is an estimate made from table 4 (p. 302) in Cole and Adkisson (1981): (0, 0.2, 0.2, 0.14, 0.13, 0.1, 0.1, 0.06, 0.03, 0.04). Adult loss rate is again assumed to be caused by density-dependent emigration as it was in the case of *C. grandis*. To simplify the assess-

Table 2

Developmental delays of the immature stages of the boll weevil, *Anthonomus grandis* (Bacheler et al., 1975, table 1, p. 809). Temperatures were held to $\pm 0.2^\circ\text{C}$, photoperiod used was 14:10 L:D

Temperature ($^\circ\text{C}$)	Eggs	L-1	L-2	L-3	Pupae
18	7.27	3.94	3.38	9.73	8.5
22	4.2	2.16	1.96	6.57	8.58
26	3.08	1.95	1.22	4.85	6.64
30	2.33	1.68	1.86	2.89	3.78
34	2.36	1.49	1.12	3.78	3.58

ment of altering attack rate functions, the only losses modeled in the host population are those due to adult emigration and parasitization in the third instar and pupae.

3.5. Model initialization

The model was initially evaluated with temperature held constant at 30°C to eliminate the effects of variable temperatures on the biological system and with the global model parameter *LOSS-RATE* set to 0.0. Setting the *LOSS-RATE* to 0.0 results in no host or parasitoid loss except where loss is modeled explicitly as was the case of both emigration or parasitization. Throughout this study, our physical unit of analysis is 10 m². The adult emigration thresholds of both insect populations were set to 100, indicating increasing emigration rates as the adult population level nears 100 per 10 m². Initial egg number for the boll weevil was set near the population limit at 100. The parasitoid was introduced into the system as adults with the initial set at 1.0 per 10 m². In subsequent model runs, the constant temperature component is replaced with real weather data (Weslaco, Texas; 1948) and the emigration threshold and fecundity rate of the boll weevil are markedly increased to 10 000 and 20-fold, respectively.

3.6. The functional response component

We compare four forms of the functional response. The Type I equation (Nicholson and Bailey, 1935) is given as:

$$N_a = N_t(1 - \exp(-a'T_tP_t)) \quad (2)$$

where N_a = number attacked; N_t = host density at time t ; a' = attack coefficient; T_t = time for attack; P_t = parasitoid density at time t .

For this example, we set $a' = 0.634$ and $T_t = 1.0$ to simulate attack rates over a period of one day (Morales-Ramos and Cate, 1992b).

Eq. 2 is compared with a Type II functional response (Royama, 1971; Rogers, 1972) given by:

$$N_a = N_t \left[1 - \exp \left(\frac{-a'T_tP_t}{1 + a'T_hN_t/P_t} \right) \right] \quad (3)$$

The terms are defined as in Eq. 2 except for the addition of T_h , the handling time required to consume the prey in the case of predators or to parasitize the host in the case of parasitoids. The values we use for Eqs. 3 and 4 are $a' = 0.743$ and $T_h = 0.013$, again according to Morales-Ramos and Cate (1992b).

$$N_a = N_t \left[1 - \exp \left(\frac{-(a'T_t)}{1 + a'T_hN_t/P_t} \right) \right] \quad (4)$$

Eq. 4 above is a modification of the Type II functional response proposed by Morales-Ramos et al. (1993). The modification is intended to produce constant probabilities of parasitization when host:parasitoid ratios are constant per unit area, a characteristic not found in Eqs. 2 and 3. This modification is intended to allow for the use of functional response values in conditions different from the experimental ones in which they were measured. However, constant host:parasitoid ratios are unlikely to occur naturally and an extensive body of literature exists on the effects of heterogeneities on host-parasitoid population dynamics (e.g. May, 1978; Hassell and May, 1988; Hassell et al., 1991).

3.7. Incorporating functional response parameters into HERMES

We can generalize the three forms of functional response into the following equation:

$$N_a = N_t [1 - \exp\{F(a', T_t, T_h, N_t, P_t)\}] \quad (5)$$

HERMES applies loss rates according to the equation:

$$Y = \exp\{-\mu t\} \quad (6)$$

where Y is the proportion surviving parasitism, μ is the rate of loss and t is time. Because we are assuming a daily time interval ($t = 1$), and HERMES uses positive values for loss rates, then $\mu = \ln Y$. The net result is that the appropriate expression to use in HERMES for calculating loss rates due to parasitism is simply:

$$\mu = F(a', T_t, T_h, N_t, P_t) \quad (7)$$

4. Results and discussion

4.1. Model verification

In order to compare the expected number of hosts attacked using the different functional response functions with loss due to parasitism calculated by HERMES, we performed six validation runs (Fig. 3). The solid circles in Fig. 3a represent field data collected by Morales-Ramos and Cate (1992b). The data consist of the numbers of weevil hosts attacked by one female parasitoid placed into a field cage over a 24-h period. The parasitoid was introduced in this manner because it is not endemic to the southern US or northern Mexico. The solid line represents the Type I equation and the dashed line is the Type II equation, using the parameters given above. When $P_i = 1$, the modified Type II equation is equivalent to the standard Type II. Fig. 3b shows the numbers attacked as simulated in HERMES using the same equations and their respective parameter values. This was performed by integrating over a one-day period and at different host densities, the rate that insects are lost through parasitism to estimate the number of hosts attacked. As shown in Fig. 3b, the numbers of hosts attacked as predicted by the Types I and II functional responses correspond closely to those calculated by HERMES using the appropriate parameter values. Although some slight differences occur in the results of the Type II function, we believe that the parameter values calculated for the functional response equations may be incorporated directly into HERMES.

Fig. 4 shows the phenology patterns for the boll weevil that are generated by the overall simulation model. To simplify the figure, first and second larval stages were pooled to comprise small larvae, as were the third instar and pupal stages to comprise the large larvae + pupae, the stages susceptible to parasitoid attack. Fig. 4a depicts the weevil life stages in the absence of the parasitoid and shows population levels that are realistic for the first generation boll weevils in the field (Summy et al., 1992). Fig. 4b shows the same boll weevil life stages with the suppression caused by *C. grandis* using a Type I attack. The decline

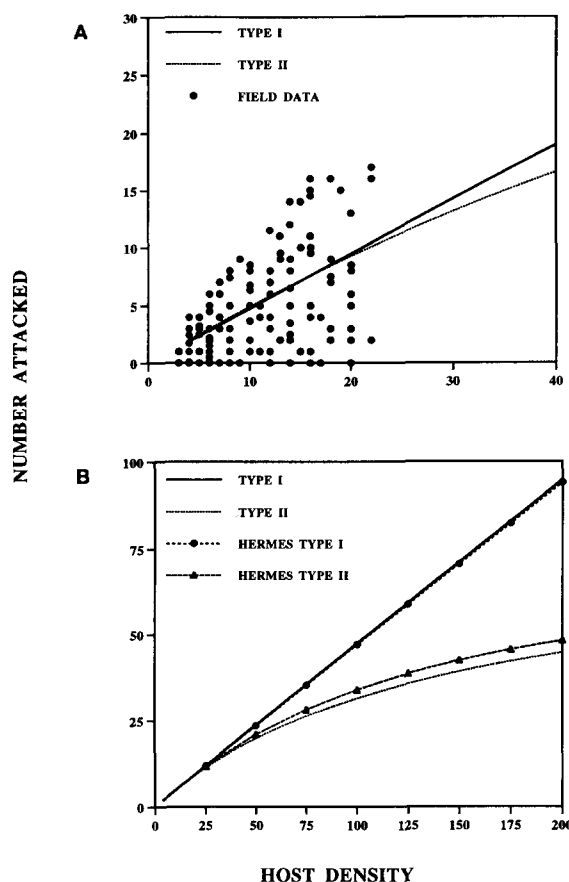


Fig. 3. Fitting functional response curves to field data. The data for (a) are taken from Morales-Ramos and Cate (1992b) which shows number of boll weevil hosts attacked over 24 h by a single female parasitoid as a function of host density. The solid line represents the fit for the Type I functional response ($a' = 0.634$, $T_i = 1.0$), and the dashed line for the Type II ($a' = 0.743$, $T_i = 1.0$, $T_h = 0.013$). When both P_i and $T_i = 1$, the modified Type II equation (Eq. 4) is equivalent to the standard Type II (Eq. 3). (b) shows the numbers attacked calculated by the HERMES system using the attack rates derived from the functional response equations (see text for details of method used).

in the susceptible (large larvae and pupal) stages is quite evident. For simplicity, we will present the population curves of only the adult stage for most of the remainder of this paper, although the reader must bear in mind the dynamics that are occurring for the other life stages in ways similar to those shown in Fig. 4a and b.

4.2. Simulation experiments

The different functional response equations were compared using the following parameters: the host population was initialized at 100 eggs; the parasitoid population was initialized at one adult; and emigration thresholds of both host and parasitoid were set at 100 per 10 m². Fig. 5a shows the adult weevil population, whereas Fig. 5b shows that of the parasitoid. The Types I and II responses produced similar curves for the weevil adults. Although the Type I response shows

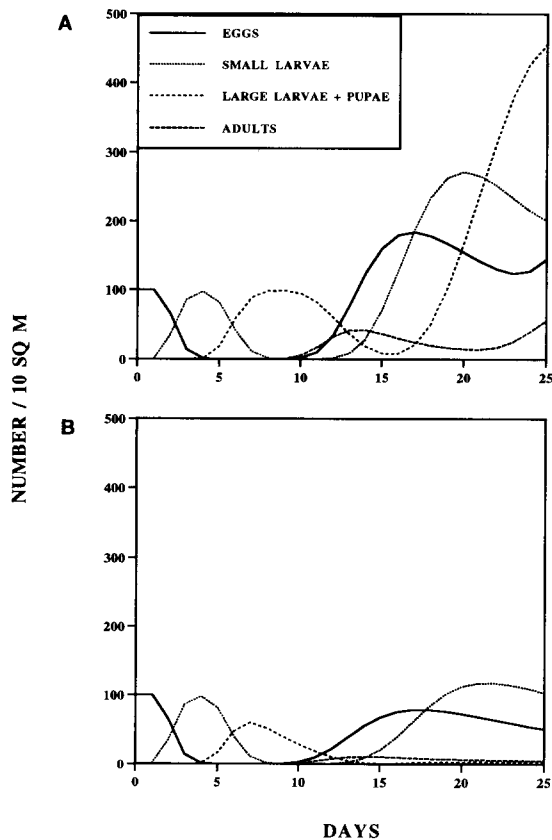


Fig. 4. The effect of a Type I functional response on all weevil life stages. (a) shows dynamics of the weevil life stages in the absence of parasitoids. This was simulated by setting the initial adult number of *C. grandis* to 0. Subsequent graphs will most often show only the adult life stages. (b) illustrates the suppression caused by *C. grandis* following a Type I response ($a' = 0.634$, $T_i = 1.0$) introduced as 1 adult at the start of the simulation.

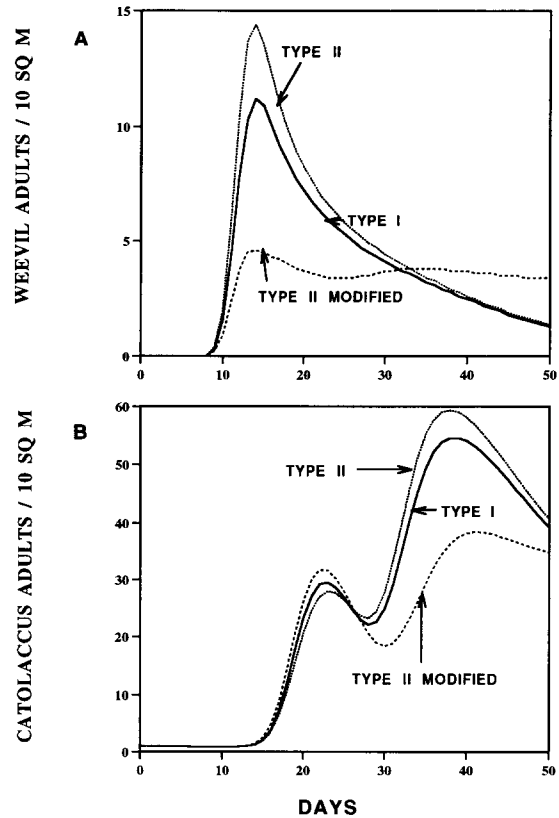


Fig. 5. Effects of Types I, II and modified Type II equations on *C. grandis* and weevil adults. The solid lines show simulated insect numbers for the Type I equation ($a' = 0.634$, $T_i = 1.0$), the dotted lines show the effect of the Type II equation ($a' = 0.743$, $T_i = 1.0$, $T_h = 0.013$). The dashed lines represent the modified Type II equation using the same parameter values as those given for the Type II.

slightly higher suppression early in the season, the curves converge at about 40 days into the simulation. In contrast, the modified Type II curve (Eq. 4) shows a reduced and more constant weevil population and lower levels of the parasitoid throughout the simulation. The parasitoid populations in Fig. 5b reveal two peaks with the modified Type II equation generating more moderate fluctuations. The general similarity of the Types I and II curves in Fig. 5 is a result of the fact that these equations are not statistically different under realistic insect densities (Morales-Ramos and Cate, 1992b).

The probability of being parasitized was estimated based on changes in the host:parasitoid ratio using initial insect densities and emigration thresholds of 100. Over a simulation period of 50 days, host:parasitoid ratios reached a maximum of just over 2:1 for Eq. 4 and about 1:1 for Types I and II. Types I and II were very similar with probabilities of attack (i.e. $1 - \exp F(a', T_i, T_h, N_i, P_i)$) constant at nearly 100% (figure not shown). Parasitism rates in excess of 94% have been achieved using augmentative releases of this parasitoid (Summy et al., 1995). The modified Type II produced an almost constant line probability of 52%. It became apparent that differences in the Types I and II equations are best revealed under conditions of host densities much higher than those found in the field or reported in Morales-Ramos and Cate (1992b). Assessing the general properties of the functional responses will require increasing host population densities to exceedingly high levels. Although unrealistic in the real world, there are several ways to increase host densities in our model for theoretical evaluation. We did so by increasing the emigration threshold for the host population to 10000 and multiplying the fecundity rate by 20. The results are shown in Fig. 6 where probability of attack is plotted against host:parasitoid ratio (on a log axis). The Type I curve shows attack probabilities still almost constant at 100% despite a fluctuation when the host:parasitoid ratios neared 10:1. The Type II curve also shows initial fluctuations but begins to decline as the host:parasitoid ratio increases beyond 10:1. The modified Type II equation show a smooth exponential decline from just above 50% to below 10% at high host:parasitoid ratios nearing 1000:1.

Fig. 6 also shows percentage parasitism as calculated using the data of Summy et al. (1992, tables 1 and 2, pp. 281 and 282, respectively). The host densities (per 10 m²) are estimated by adding together the densities of 3rd instars and pupae of the boll weevil. The parasitoid density is estimated by using the cumulative densities of parasitoid released during the growing season. The latter is a crude estimate of parasitoid density because it is simply a measure of parasitoids

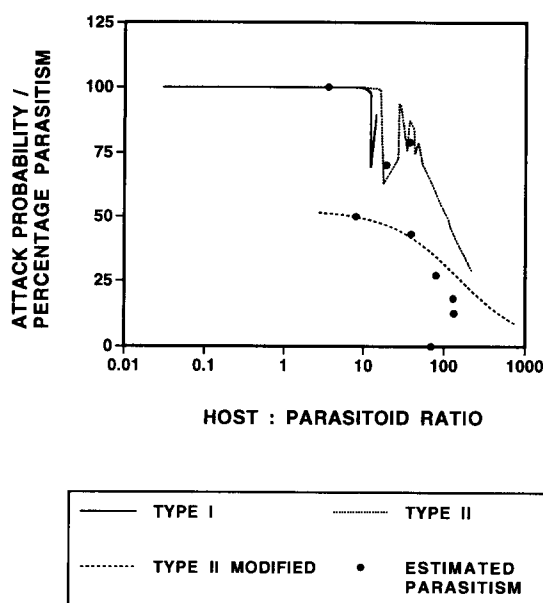


Fig. 6. Effect of host:parasitoid ratio (drawn on a log scale) on probability of attack. The functional responses were parameterized as in Fig. 5 (Type I: $a' = 0.634$, $T_i = 1.0$; Type II and modified Type II: $a' = 0.743$, $T_i = 1.0$, $T_h = 0.013$) and the model was run for 50 days.

released in an augmentative program rather than densities measured by monitoring the field during the season. These host:parasitoid ratios are plotted (solid circles) against corresponding parasitism found at that point in the season (Summy et al., 1992, table 4, p. 284). Parasitism as an estimate of attack probability indicates that 100% probability of attack occurs very rarely, in this study, for only one case when the host:parasitoid ratio was 3.5:1. Probability of parasitism is usually much lower, often either close to or below that predicted by the modified Type II. The estimated host:parasitoid ratio also attained a maximum in excess of 130:1, as compared to less than 2:1 using initial model parameters. This further supports the conclusion that simple Type I or II equations are highly inaccurate in their estimates of parasitoid attack in a simulation model. Indeed, the inapplicability of Types I and II equations in simulation models was a major stimulus behind the derivation of the modified Type II equation (Morales-Ramos et al., 1993).

It appears that the Types I and II equations and their parameterization using functional response experiments often produce attack rates that are unrealistically high when incorporated into a dynamic simulation model. Perhaps this is because functional response experiments are conducted under such ideal conditions and durations for parasitoid search that they are unrealistic in the long term. Another possibility is that host densities are unrealistically high in many functional response experiments (Wiedenmann and Smith, 1993), although that should not be the case in this study because of the use of the field functional response experiment to parameterize the model. Thus, there appear to be two approaches to manipulating the functional response so that it may be incorporated into a simulation model: introducing modifications, such as that proposed in Morales-Ramos et al. (1993) and/or by mediating the functional response through the effects of external (environmental factors). We pursue this alternative using temperature as the mediating influence.

4.3. Modeling temperature-dependent functional response

The effect of temperature on functional response was shown in the classic paper by Holling (1959) on predation and parasitism. Because there are no data on temperature effects on the functional response of *C. grandis*, we must speculate on this relationship in order to examine its effects on attack rates within and between days. We will assume that optimal temperature for *C. grandis* parasitization is 30°C. Other temperatures within the range of 15°C to 35°C will reduce the attack rate by a specified fraction and temperatures below 15°C will have attack rates reduced to a constant 0.1 of the optimal and temperatures above 35°C will have attack rates reduced to a constant 0.5 of the optimal. Accordingly, we used the following lookup table for coefficients of attack rate as a function of temperature: (15° 0.1, 20° 0.4, 25° 0.7, 30° 1.0, 35° 0.5). This table is not meant to be an exact representation, but rather a reasonable approximation of the reduction in attack rate caused by temperature.

The effect of a temperature-dependent functional response component was easily incorporated into the model by adjusting the attack rate by the temperature-dependent coefficient calculated at each time step within the model using the table given above. We also added a *weather* component which consists of a maximum–minimum temperature file for Weslaco, Texas in 1948. Given temperature maxima and minima, HERMES fits a sine wave through the data points to allow for interpolating temperature at any time during the course of a simulation day. An example of the effect of temperature on the modified attack expression is shown in Fig. 7 for Julian days 279 and 280.

Fig. 7a shows three curves: temperature interpolation by HERMES routines, the adult female parasitoid population, and the ‘unadjusted’ attack rate. The latter is the attack rate calculated using a Type II equation that is not temperature-dependent, and was used as a basis for comparison. The line for attack rate reflects the increase in attack at higher temperatures. The depressions in attack rate found near the peaks are caused by temperatures as they exceed the 30°C optimal. Calculated attack rates (Fig. 7b) for the entire female parasitoid population are compared to the per capita attack rate. The declines in attack rate are not due to decreases in the parasitoid population because the curve for the per capita attack rate reveals the same trends as those for the entire parasitoid population. This method of adjusting attack rates may also be applied for simulating diurnal patterns of activity under the assumption that natural enemy activity occurs only during certain portions of the 24-h daily cycle. In contrast, the unadjusted attack rate simply reflects the current level of the parasitoid population.

Host population levels simulated using a temperature-dependent Type II functional response were compared to host population levels calculated using simple Type I and II equations and the respective parameters mentioned previously, and finally in the absence of a parasitoid population. For these simulations, the emigration thresholds for both host and parasitoid were set at 100, the initial egg number of the host was set at 100, and the parasitoid population was initial-

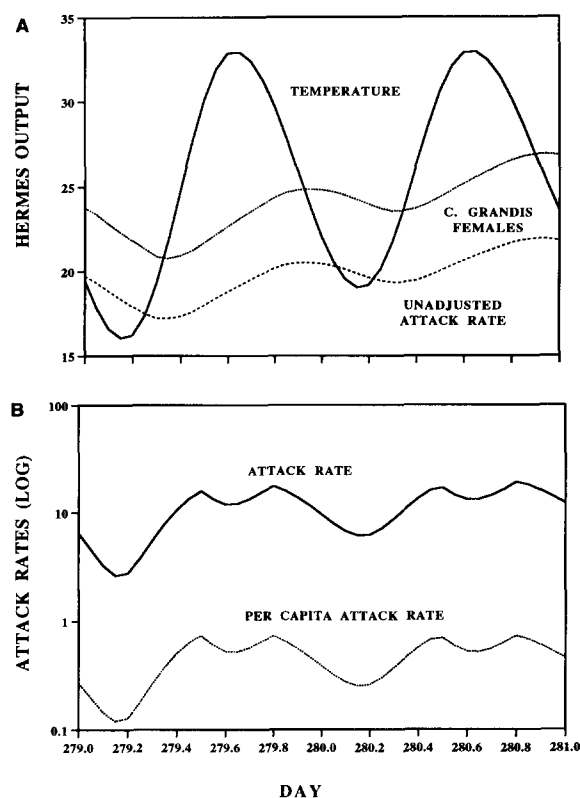


Fig. 7. Effect of a temperature-dependent Type II equation on daily attack rates (Julian days 279 and 280). The solid line represents the temperature sine wave calculated using the maxima and minima temperature file for Weslaco, Texas (a). The dotted line represents the female parasitoid population and the dashed line is the attack rate for the model run using a Type II equation without the temperature-dependent effects. (b) shows that attack rates (Eq. 7 in the text) and per capita attack rates and reflects the increased attack rates at higher temperatures as well as declines in attack when temperature exceeds the 30°C temperature for optimal parasitization.

ized as one adult (except for the simulation in the absence of parasitism, in which case it was set to 0). In these situations, the model predicts two distinct peaks in the populations of susceptible hosts (3rd instar and pupae), with the absence of parasitism resulting in further growth in the host population (Fig. 8). All three forms of functional response produce marked suppression of the host, again revealing that the parasitoid has the biological potential to control the boll weevil under

these conditions. The Types I and II response equations produced curves that are very similar, because the host density per parasitoid is usually within the range where the Types I and II curves are not significantly different (Fig. 3a). However, incorporating hypothetical effects of temperature on the Type II response results in marked differences as compared to the standard Type II equation. The differences arise because the fluctuating temperature is rarely at the 30°C optimum and causes suboptimal attack rates. The Weslaco, Texas weather file used in these simulations is for that of a subtropical area (26°10'N latitude, 97°58'W longitude). Although the effect of temperature on attack rates is hypothetical and not based on experimental data, the simulations indicate that temperature variability may have a profound effect on parasitism rates and thus on the

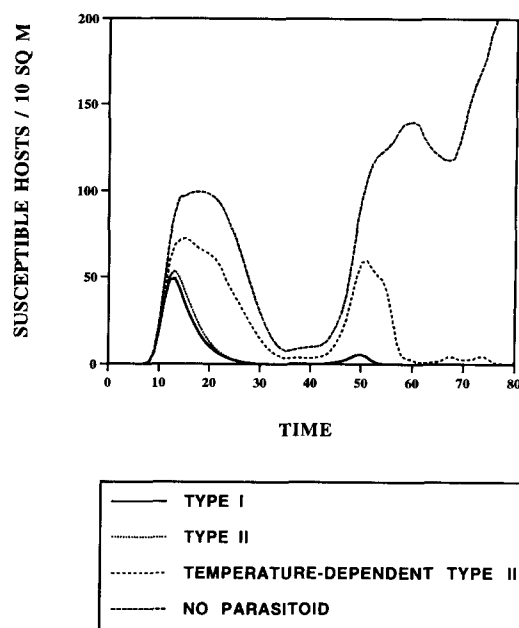


Fig. 8. Effect of Types I and II and temperature-dependent Type II functional response equations and the absence of parasitoids on the numbers of susceptible hosts. The solid line represents adult weevil populations as affected by a Type I equation ($a' = 0.634$, $T_i = 1.0$). The dotted line represents a Type II equation ($a' = 0.743$, $T_i = 1.0$; $T_h = 0.013$) and the wide dashed line a temperature-dependent Type II equation with the same parameter values. The narrow dashed line shows the susceptible hosts in the absence of parasitism.

population dynamics of this host–parasitoid system. More detailed simulation models of the boll weevil–*C. grandis* system may require the collection of temperature–dependent functional response data to be accurate representations of this system.

5. Conclusions

Our attempts to model parasitoid attack by using the functional response equation have forced us to re-evaluate the definition and utility of functional response experiments. The unrealistically high attack rates yielded by these equations when incorporated into dynamic simulation models are probably caused by two factors:

1. Functional response experiments are performed under conditions highly conducive to attack because the hosts and their natural enemies are spatially confined and placed in constant conditions favorable to attack.
2. Functional response experiments are often conducted using unrealistically high host densities.

Functional response experiments performed in the laboratory are usually conducted under optimal physical conditions. Temperature and humidity are regulated, and the insects are shielded from the vagaries of the environment. Such optimal laboratory conditions rarely occur in the field. Simulation models of predator–prey or host–parasitoid systems rarely incorporate diurnal patterns such as temperature and light regimes which obviously affect the searching behavior and general activity of natural enemies. Other less predictable environmental variables as rainfall, wind or insecticidal drift will also affect functional response, perhaps to the point of determining whether or not the natural enemy searches at all.

In many experiments, natural enemies are provided hosts in densities several orders of magnitude greater than those found in field conditions (O'Neil, 1990). The superabundance of hosts results in attack rates far exceeding those that occur in the field. In fact, Wiedenmann and Smith (1993) found that a simple linear regression is indistinguishable from a functional response in

Cotesia flavipes (Cameron) (Hym.: Braconidae) attacking *Diatraea saccharalis* (F.) (Lep.: Pyralidae) when the experiment was conducted using low host densities in field cages. The parameter values of a' , T_h and T_i used in this model were also derived using field cages in order to produce realistic estimates. However, field cage experiments have their own limitations because of the confinement of hosts and parasitoids. The need to control host and parasitoid densities by confinement may preclude emigration or escape by hosts and removes the parasitoids' need to locate the host plant, which is usually the first requirement for successful attack.

There appear to be two possible alternatives to address the problem: The first is to modify the functional response equation such that the probability of attack becomes less dependent on parasitoid density (e.g. Morales-Ramos et al., 1993), or to change its parameters from constants to functions of external factors such as temperature (e.g. Mack and Smilowitz, 1982a, b). A related solution is to mediate output of the attack equation by making it responsive to external environmental or diurnal variables as we attempted to demonstrate in this work.

Studying the effects of these factors on parasitoid behavior will not only enhance our understanding of the biology involved, but also enable us to build increasingly realistic models of biological control life systems. Clearly, not all simulation models need to incorporate all of these mechanisms and will be sufficient for their purposes without the added detail and data that the more comprehensive models will require. We believe, however, that developers of simulation models must be aware of these diurnal events and environmental variables in deciding whether or not they impact significantly the systems they seek to model.

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